

## THE TERMINATION OF OPTIC FIBRES IN THE LATERAL GENICULATE BODY OF THE MONKEY

BY P. GLEES AND W. E. LE GROS CLARK

*Department of Anatomy, University of Oxford*

THE classical observations made by Henschen (1897, 1898) and Winkler (1912, 1913) on the localization of optic fibres in the lateral geniculate body of the human brain were amplified by Rönne (1913, 1914). This author published a series of clinical cases of alcoholic and diabetic amblyopia which provided definite evidence that the central part of the geniculate body receives fibres of macular origin while the medial and lateral portions are concerned with the reception of impulses from the peripheral zone of the retina. This conclusion was confirmed, on the basis of experimental work on monkeys, by Brouwer (1923) and Brouwer & Zeeman (1925). Brouwer & Zeeman made small circumscribed lesions in the retina and followed the degenerating fibres by the Marchi technique. They found that the macular fibres end in a large central part of the geniculate body, and that fibres from the upper and lower halves of the peripheral retina end respectively in the medial and lateral margins of the nucleus. It is clear, however, that the Marchi method can give only an approximate indication of the site of termination of the optic fibres. In the experiments of Brouwer & Zeeman, for example, it showed nothing of the relation of crossed and uncrossed fibres to alternating cell laminae in the geniculate body—a relationship which had been established in 1920 by Minkowski. Minkowski's conclusions were based on the transneuronal degeneration which follows enucleation of one eye or section of one optic nerve. Le Gros Clark (1932) confirmed these observations on the monkey and first showed that a similar arrangement also obtains in the human brain. The relationship may be expressed simply by the statement that, if the six cell laminae of the lateral geniculate body are numbered from the hilum of the nucleus (Text-fig. 1), crossed retinal fibres terminate in laminae 1, 4 and 6, while uncrossed fibres end in laminae 2, 3 and 5 (Le Gros Clark, 1941). Further proof of this arrangement in the human brain was provided by Hechst (1933).

In 1934 Le Gros Clark & Penman sought for more accurate information on the retinal projection in the lateral geniculate body, using the phenomenon of transneuronal degeneration as an index of the actual site of termination of fibres from different parts of the retina after effecting small circumscribed lesions in the retina. In these experiments it was found that the cell atrophy in the geniculate body is always quite localized and sharply defined, suggesting that the projection of the retina on the lateral geniculate body at least approximates to a point-to-point relationship.

In spite of these studies, nothing is yet known of the actual morphology of the terminals of the optic fibres in the lateral geniculate body of higher

mammals, nor is it known with how many geniculate cells each optic fibre comes into contact. Indeed, the inference that crossed and uncrossed fibres end in different cell laminae has depended hitherto entirely on the indirect evidence of transneuronal degeneration. But this type of degeneration in itself raises new problems regarding the terminal relation of optic fibres and geniculate cells, for it demonstrates that these cells undergo marked and rapid atrophy if the afferent fibres conveying the functional stimulus are sectioned. A slight degree of cell atrophy has been observed in the geniculate body of the cat after section of the optic nerve, but marked and rapid transneuronal degeneration has only been recorded in the monkey and Man. In lower mammals it either does not occur at all, or is so slight as to be not readily detected on direct observation. In the monkey, such transneuronal degeneration does not appear to occur in the ventral nucleus of the thalamus after lesions involving the medial fillet (according to our unpublished observations), and, indeed, it seems doubtful whether it occurs anywhere else in the brain of this animal. Foerster *et al.* (1938) reported a transneuronal degeneration in certain cells of the spinal cord following section of posterior roots, but these observations are perhaps open to a different interpretation, for the cells which were stated to show atrophy were few and scattered, and those who have attempted to plot the position of chromatolytic cells in the spinal cord after section of spinal nerve roots will agree that it is often a matter of great difficulty to distinguish true chromatolysis from the variable appearance of normal cells. Schimert (1938) was unable to confirm the statements of Foerster *et al.* with regard to the alleged transneuronal degeneration in the spinal cord.

The rapid transneuronal degeneration which occurs in the lateral geniculate body of the monkey suggests that the terminal relation between the optic fibres and the geniculate cells is of a particularly intimate nature. The present study was initiated in order to inquire into this question. The only observations hitherto recorded on the mode of termination of optic fibres in the lateral geniculate body are those of Kölliker (1896) on the mouse, and Tello (1904) and Cajal (1911) on the cat. Kölliker merely reports that fibres end in a brush formation. According to Tello the optic fibres enter the hilum of the geniculate body in the cat and ramify in the three cell layers of the nucleus. As soon as a fibre enters its particular layer it divides into a fusiform reticulum which, as he says, resembles a cypress tree. However, the Golgi technique used by Tello is not adequate for demonstrating the precise relation of a single optic fibre to the geniculate cells, nor the actual morphology of the ultimate fibre ending.

#### MATERIAL AND METHODS

Normal and experimental material was used for the study of the nerve endings in the lateral geniculate body. The experimental material was provided by five monkeys in which one optic nerve had been sectioned, the animals being killed 3, 7, 17, 18 and 46 days after operation.

A variety of silver-impregnation methods were used for the demonstration of nerve fibres and their terminals. Of these the following technique proved very successful in the study of degenerating terminals:

1. Fixation in 10 % formalin—Pyridine 4 drops per 100 c.c. for 6–8 days.
2. Wash in distilled water 12 hr.
3. 0.4 % NaOH 12 hr.
4. Wash in distilled water 12 hr.
5. 10 % AgNO<sub>3</sub> 12 hr.
6. 1 min. wash in distilled water.
7. 15 min. in Hortega's silver carbonate.
8. Reduce in 10 % formalin.
9. Clear and mount with or without toning.

Another very useful method which was employed was that of Bielschowsky-Gros, as recommended by Schimert (1938). Frozen sections were also stained with gallocyenin, in order to determine the disposition and pattern of the cell laminae of the geniculate body for comparison with the silver sections.

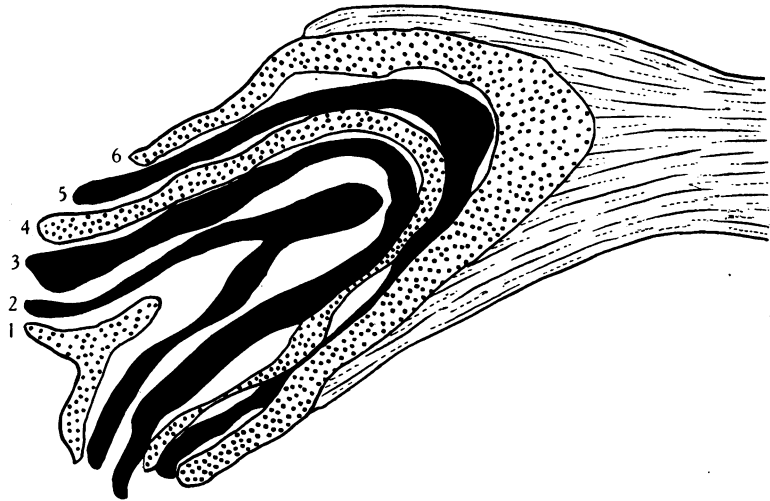
#### OBSERVATIONS

Although in the normal and experimental material sections were made in a variety of planes, it was found most useful, in order to follow the course of the optic fibres, to cut the geniculate body in a vertical plane along the axis of the optic tract. A diagram of such a section is shown in Text-fig. 1. From the diagram it becomes at once clear that the bulk of the optic fibres do not enter the lateral geniculate body from the hilum; on the contrary, they penetrate the curved cell laminae on their convex aspect, many of them passing through the greater part of the geniculate body in order to reach the cells in the region of the hilum. Silver sections show that, on entering the nucleus, the optic tract splits up into fairly well-defined fasciculi, and from these the individual fibres turn out abruptly to enter the various cell laminae. From their direction it is clear that in order to reach lamina I (bordering the hilum) many of the fibres must pass through all the other cell laminae. It is also clear that the course taken by the entering optic fibres bears no relation to the fibre layers which intervene between the cell laminae of the lateral geniculate body. These fibre layers, indeed, are formed not by the optic fibres but mainly by the geniculo-cortical fibres. This is demonstrated clearly enough in those cases of congenital anophthalmos in which no optic tract fibres are present. In such cases, Weigert sections of the lateral geniculate body show that laminae of medullated fibres are still present in this nucleus (see, for example, Fig. 4 in a recent paper by Whitnall & Norman, 1940).

An examination of the normal geniculate body in silver-impregnated material shows such a density of nerve fibres among the cells of the nucleus that it is quite impossible to identify and follow individual optic fibres to their termination. But this material demonstrated the existence in relation to some of the cells of the geniculate body of what appear to be terminal boutons of

a characteristic type. As shown in Pl. 1, fig. 1, these boutons are in the form of very fine rings. They are by no means easy to find, but where present each ring lies in contact with the cell body and in no instance was it possible to demonstrate a terminal bouton related to a dendritic process. Moreover, a careful scrutiny failed to show any nerve cell in the geniculate body which received more than one terminal bouton.

It seemed probable that these terminal boutons were the end-formations of the optic fibres, but of this no proof could be obtained in normal material. It was therefore decided to see whether after section of the optic nerve the boutons showed any of the characteristic degenerative changes which have been observed to occur in the spinal cord after section of descending tracts (Hoff, 1932; Gibson, 1937).



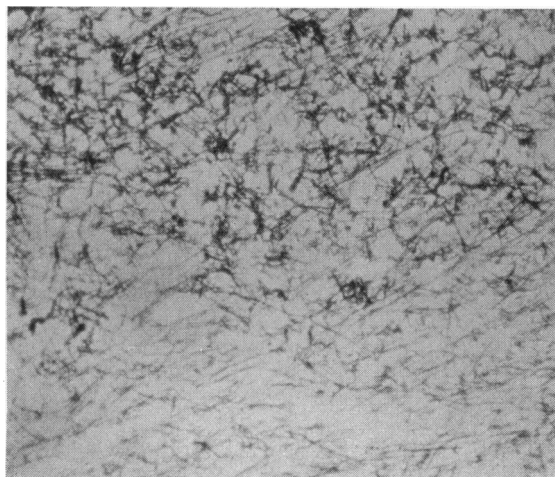
Text-fig. 1. Projection drawing of a sagittal section through the lateral geniculate body of a rhesus monkey, showing the termination of the optic tract and the disposition of the cell laminae. It will be noted that in this plane the hilum of the lateral geniculate body is at its caudal end, while the optic tract fibres penetrate it from its convex aspect.

*Experiment O.M. 502.* In this experiment the monkey was killed 3 days after section of the right optic nerve. In the right (ipsilateral) geniculate body it is quite evident, even under a comparatively low-power objective, that there are many fibres in laminae 2, 3 and 5 which are swollen and which show a much deeper impregnation when compared with similar fibres in those laminae (1, 4 and 6) which receive crossed optic fibres. With an oil-immersion lens it can be seen that the ring of the terminal boutons is in many instances thickened, somewhat enlarged, and stained more densely than in normal preparations. These changes are also to be observed in the left geniculate body, but they are here found in laminae 1, 4 and 6. The interior of the ring-like boutons in these laminae is often found to be filled with a dense, opaque mass which on close

scrutiny appears to be composed of a very fine neurofibrillar network (Pl. 1, fig. 2). In other instances the boutons have become converted into small solid, black end-bulbs.

Frequently in the affected laminae a fibre is found branching in terminal ramifications, and in such a case the fibre at the site of its division, and also its branches, are conspicuously thickened and very deeply stained (Pl. 1, fig. 3). This appearance, indeed, is a much more obtrusive feature of the affected laminae than the end-bulbs, for although the latter are clearly undergoing degeneration they are at this stage still relatively small.

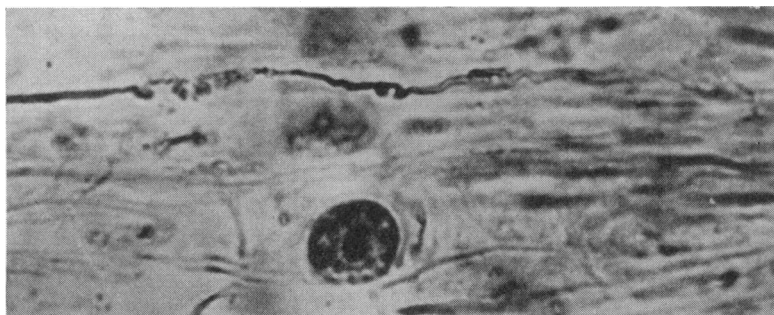
*Experiment O.M. 503.* In this experiment the animal was killed 7 days after section of the right optic nerve. Lower power examination of silver



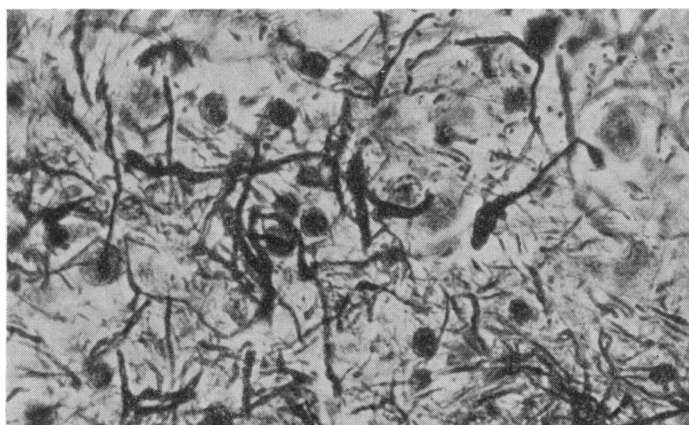
Text-fig. 2. Section through a part of the lateral geniculate body from Experiment O.M. 503, showing above a cell lamina filled with degenerating terminals of optic fibres, while below is a normal lamina. Silver impregnation.  $\times 150$ .

sections shows that laminae 1, 4 and 6 of the contralateral geniculate body and laminae 2, 3 and 5 of the ipsilateral nucleus stand out in strong contrast with the other laminae by reason of the dense staining of the fibre plexuses which pervade them (Text-fig. 2). With a high-power objective the meaning of this contrast becomes clear. From the optic fasciculi which penetrate the geniculate body, thickened fibres can be seen turning out at right angles to enter the affected cell layers and here undergo a terminal branching. As is seen in Text-fig. 3 the degenerating fibres of the optic fasciculi present an irregular contour and also show an incipient fragmentation. Other fibres are distinguished by a cylindrical swelling in their course (Pl. 1, fig. 4). When an optic fibre approaches the group of geniculate cells in relation to which it is destined to end, it divides into several branches. The mode of branching is shown in the photomicrograph in Pl. 2, fig. 1. In this particular instance, the optic

fibre first gives off two rami and later divides into two branches. Of the latter, one ends in an enlarged end-bulb; the other forms three small branches terminating in smaller bulbs. Each of the end-bulbs is in contact with the body of a nerve cell. In general the boutons of the affected laminae are grossly degenerated, and often appear as large, elongated and densely black bulbs, which form conspicuous objects even under low-power objectives (Text-fig. 4).

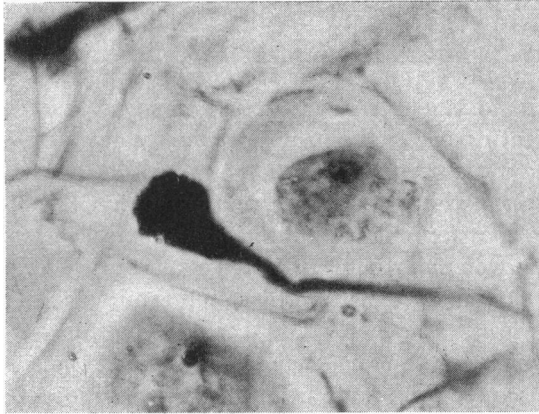


Text-fig. 3. Section of a fasciculus of the optic tract from Experiment O.M. 503, showing a degenerating axone which is thickened and irregularly coiled.  $\times 900$ .

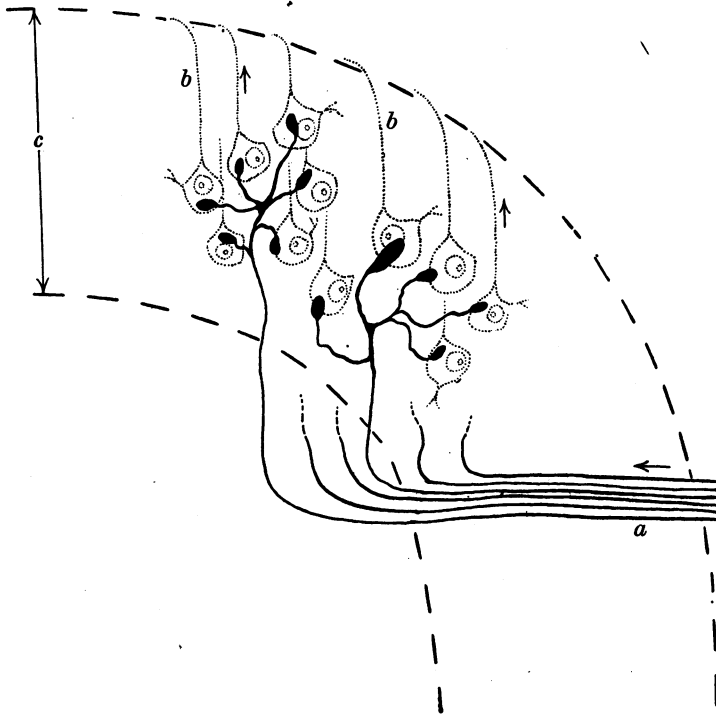


Text-fig. 4. Section through a cell lamina of the lateral geniculate body from Experiment O.M. 503, showing enlarged degenerating boutons and thickened terminal fibres of the optic tract.  $\times 400$ .

There is, however, considerable variation in the extent of the degeneration of different end-bulbs, some remaining quite small. Occasionally, also, an apparently normal bouton with a typical ring form can be found in connexion with one of the terminal optic fibres (Pl. 1, fig. 6). Such endings are more frequent in the large-celled laminae (1 and 2). In these laminae the cells are distinguished not only by their size but also by their more numerous dendritic processes and their deeper staining with basic dyes. The functional significance



Text-fig. 5. An enlarged terminal bouton lying in relation to the body of a geniculate cell, from Experiment O.M. 503.  $\times 2000$ .



Text-fig. 6. Diagram (constructed from a study of the sections of Experiment O.M. 503) showing the termination of optic fibres in relation to the cells of the lateral geniculate body. A fasciculus of optic fibres (a) is shown entering the geniculate body from the right. From this fasciculus, individual fibres turn out at right angles to enter their appropriate cell lamina (c). Each fibre ends in a spray of 5-6 branches, and each of these terminates in an end-bulb which lies in contact with the body of one geniculate cell. The axones of the geniculate cells (b) pass into the fibre laminae of the nucleus and run through these to reach the optic radiations.

of these morphological differences is obscure, for, as far as is known, the connexions of the cells of these laminae are the same as those of the other small-celled laminae.<sup>1</sup> It may be noted, however, that in the large-celled laminae no terminal branching of the optic fibres was observed. The enlarged and solid degenerating end-bulbs provide the only objective evidence here of the section of the optic nerve fibres.

A careful study of the sections from experiments O.M. 502 and 503 leads to the conclusion that (except possibly in the large-celled laminae) each fibre when it has turned out at right angles from the optic fasciculi entering the geniculate body commonly divides into 5 or 6 rami, each of which is related to one geniculate cell. In other words, each of the fibres from the retina is related at its termination to 5 or 6 geniculate cells. It is also to be noted that in no instance was any cell found to be in contact with more than one end-bulb, and that the end-bulb is always in contact with the cell body and not with its dendritic processes (Pl. 1, fig. 6).

In the other experiments (in which the animals were killed 17, 18 and 46 days after section of one optic nerve), the silver preparations provide no further details regarding the mode of termination of the optic fibres. The main optic fasciculi, and also the laminae whose afferent fibres had been interrupted, show an abundance of grossly degenerating axones, and no normal or degenerating boutons are to be found in the affected laminae of the geniculate body. In all these cases, transneuronal degeneration in the geniculate body is conspicuous.

#### DISCUSSION

The demonstration of typical ring-shaped boutons in the lateral geniculate body of the monkey, similar to those which occur in relation to the motor cells of the spinal cord, at once suggested the possibility of studying the optic terminals by reference to the degenerative processes which they might undergo after section of the optic nerve. The value of degenerating boutons for the determination of the precise site of termination of fibre tracts in higher mammals was indicated by the work of Hoff (1932) on the relation of pyramidal tract fibres to anterior horn cells. In 1937 Gibson reported an experimental study of the 'bouton method' and provided a useful historical survey of the subject. In 1938 Schimert was able by this method to establish the site of termination of the fibres of the vestibulo-spinal tract in the cat. For this purpose he recommended the Bielschowsky-Gros technique of silver impregnation. Schimert considers that the appearance of the end-bulb itself is not always a safe criterion of degeneration, unless it is accompanied by degenerative changes affecting the terminal fibre which carries it. In a recent paper, Phalen & Davenport (1937) put forward some justifiable criticisms regarding the validity of the method, for they point out that normal boutons show considerable

<sup>1</sup> Balado & Franke (1937) have stated their opinion that the cells of the large-celled laminae of the geniculate body project on to the superior colliculi. However, it is a fact, as Poliak (1933) has noted, that all the cells undergo retrograde atrophy following removal of the visual cortex.

variation in their contour, size and appearance. They conclude that it can only be employed successfully for locating synaptic connexions if the degenerating end-bulbs are massive in their extent. Still more recently, Barnard (1940) has strongly criticized the observations of Hoff, Gibson and Schimert. This author was unable to demonstrate any degenerative changes in the end-bulbs related to the cells of the spinal cord. No variation from the normal was observed below the level of the lesion after hemisection of the cord, or after section of the dorsal roots. The present communication deals only with degenerative changes in the lateral geniculate body, and therefore Barnard's paper hardly calls for discussion here. We would only say that we have found some difficulty in appraising this paper (and also some other papers dealing with the same subject) because it lacks the objective evidence of photomicrography. We would, however, suggest that, if Barnard's conclusions should lead anyone to doubt whether end-formations ever undergo the degenerative changes which have been described by previous authors, the simple experiment of sectioning one optic nerve in a monkey should be performed, and the lateral geniculate body examined 7 days later by appropriate and critical silver methods. From the description in the present paper of the boutons in the lateral geniculate body 7 days after section of one optic nerve it will be apparent that the degeneration is massive, for the affected laminae are scattered with a profusion of grossly degenerated end-bulbs. Moreover, their presence is made the more conspicuous by comparison with the alternating laminae in which the boutons remain normal in appearance (see Text-fig. 2). The synaptic connexions of the lateral geniculate body are of course much less complex than those of the cells in the spinal cord, for the geniculate cells probably serve the single function of a relay between the retinal fibres and the visual cortex. Indeed, it is just because of its simple synaptic organization that this nucleus provides much more favourable material than the spinal cord for the general study of the degenerative changes which occur in end-formations after axonal interruption.

The initial degenerative changes in the terminal boutons are a thickening and heavier staining of the ring formation, a slight enlargement, and a filling of the interior of the ring with a silver-reducing substance. As already noted the latter appears to be composed of a close-meshed fibrillar network. It is our impression, in agreement with the opinion previously expressed by Bielschowsky (1935), that in normal boutons the interior of the ring is filled with an extremely fine membrane of neurofibrillar structure—so fine that it is usually difficult to detect. If this is so the 'solidification' which occurs in degenerating boutons is simply due to a thickening of this membrane. As degeneration proceeds the boutons become markedly enlarged to form round, oval and elongated fusiform bodies staining a dense black.

It is of some importance to note that the initial process of degeneration which follows interruption of the optic fibres is not confined to the boutons; it also affects the fibre at the site of its terminal division as well as its telodendritic processes. These become irregularly swollen and stain deeply with

silver impregnation. Indeed, in the earlier stages this degenerative change is much more conspicuous than that which affects the boutons themselves. Moreover, it serves to bring into prominence the form and disposition of the terminal branching of the optic fibres and allows this branching to be seen in the midst of the profuse plexus of fibres which pervades the whole of the geniculate body. In a normal silver preparation it is quite impossible to distinguish this end-formation.

It should be emphasized that the boutons in the normal geniculate body of the monkey are difficult to find in comparison with those of the spinal cord, and they appear to be much fewer than the enlarged bulbs in the degeneration experiments. It seems that this is probably due to the fact that (1) only a single bouton is related to each geniculate cell, and (2) their minute size and light staining, as well as the fact that they can only be defined in certain planes of section, make them difficult to detect. On the other hand, while we have the impression that the enlarged bulbs of the experimental material represent a degenerative process occurring in normal ring-shaped boutons, this does not exclude the possibility that they may also be produced by a local thickening of free terminals. We can only say, however, that such free terminals were not visible in the silver preparations. In any case, it may be observed that the precise mode of formation of the enlarged end-bulbs does not affect the main thesis of this paper, which is concerned with the terminal relation of optic fibres to geniculate cells.

A study of the experimental material makes it evident that the optic fibres penetrate the lateral geniculate body in an antero-posterior direction in discrete fasciculi. From the latter individual fibres turn out at right angles to enter their appropriate cell laminae. With the possible exception of the large-celled laminae, each fibre ends by breaking up into a spray of five or six fine branches each of which ends in a terminal bouton in contact with the body of a geniculate cell (Text-fig. 6).<sup>1</sup> Moreover, it seems probable that no cell in any of the laminae of the geniculate body receives more than one bouton. Thus the cells of the lateral geniculate body stand in strong contrast to the motor cells of the spinal cord which have multiple contacts with terminal boutons.<sup>2</sup> Indeed, Barr (1940) has estimated that in the spinal cord of the cat each single anterior horn cell may have in contact with it as many as a thousand terminal boutons. This is to be explained partly by the fact that the motor cells of the spinal cord are served by many different fibres conveying many different types of impulse. On the other hand, as already noted, it seems that the cells of the lateral geniculate body have one function only to perform—to serve as simple relays for retinal impulses on their way to the visual cortex. It may be noted

<sup>1</sup> We cannot affirm from our preparations that the relation of one optic fibre to 5-6 cells in the lateral geniculate body is invariable; but this seems at least to be the common arrangement.

<sup>2</sup> For purposes of comparison, we have prepared normal control material of the spinal cord, medulla and cerebellum, using the same silver techniques as those employed for the lateral geniculate body. In all these sections we have been able to demonstrate terminal boutons and end-formations corresponding precisely with the classical descriptions given by previous authors.

that another example of a single relay station is provided by the trapezoid nucleus in the hind-brain, which appears also to serve only one afferent system.

The only demonstrable boutons in the lateral geniculate body are those of the optic fibres. This raises the interesting question whether the geniculate cells do in fact receive any other afferent fibre systems. The speed with which transneuronal degeneration occurs in the lateral geniculate body (it is already evident in experiment O.M. 503, 7 days after section of the optic nerve) suggests that this is probably not the case, for it is difficult to explain such a rapid effect except on the basis of the removal of all the afferent stimuli on which the functional activity of the cells depends. The only other afferent fibres to the lateral geniculate body which have hitherto been described are descending connexions from the occipital cortex. The existence of such cortico-geniculate fibres seems to have been accepted by several authors as a part of a general cortico-thalamic system whereby the various thalamic nuclei are brought under the functional control of those areas of the cortex to which they project sensory impulses. In regard to the lateral geniculate body, at least, the evidence for such a descending connexion is meagre.

Biernond (quoted by Walker, 1938) described corticogeniculate fibres in the rabbit on the basis of Marchi preparations, and Mettler (1935), with the same technique, affirms their presence in the monkey. On the other hand, Poliak (1932) doubts their existence in the monkey, and Barris (1935) was quite unable to detect them in the cat. Clearly this is a matter which demands further investigation with a technique which is more critical than the Marchi method. It may be observed that, if the optic fibres are the only afferent fibres of the lateral geniculate body, and no other synaptic connexions exist, it is difficult to understand the purpose of the dendritic processes of the geniculate cells for, as we have seen, the optic terminals end in contact with the cell body, and the existence of intercalated neurones in the nucleus seems to be excluded by the total degeneration of the geniculate body following removal of the visual cortex. It is possible, however, that the dendritic processes of the geniculate cells may receive collaterals from the geniculostriate fibres, such as have been described by Tello (1904) in the cat. As already mentioned, in O.M. 503 we were able to find occasional end-bulbs of apparently normal appearance, and it might seem possible that these are the terminations of a fibre system other than the optic tract. We think that this is almost certainly not the case, however, for it was generally possible to trace such end-bulbs in connexion with a main optic fibre. Moreover, further evidence that they belong to fibres of retinal origin is provided by the fact that all the end-bulbs related to the bodies of the appropriate geniculate cells have disappeared in the experiment in which the optic nerve was cut 17 days before death.

The inference that (with the possible exception of the large-celled laminae) the receptive unit of the lateral geniculate body commonly consists of a small

and discrete group of 5–6 cells is reflected in the cytoarchitecture of the nucleus as it appears in methylene blue preparations, for it is frequently to be observed that the cells tend to occur in clumps of about the same number. It also is in approximate harmony with the earlier observations of Cajal (1911) and Tello (1904) on the lateral geniculate body of the mouse and cat; in these animals each optic fibre was found to form a plexus of terminals in the meshes of which 6–8 cells are embedded. Neither of these authors described terminal boutons; indeed, Cajal (1935) specifically denies their existence in the lateral geniculate body. But they both employed the Golgi method of impregnation, a method which is usually not adequate for the demonstration of terminal boutons. In addition, Cajal confined his studies to young animals and he points out that in the spinal cord the small discrete end-bulbs are late formations, being preceded in development by a diffuse reticular termination. Further, it is possible that the relation of optic fibres to the geniculate cells may be different in the mouse and cat, related to the fact that transneuronal degeneration in the lateral geniculate body of lower mammals either does not occur or is relatively slight. It may be noted that Cattaneo (1923) described reactive phenomena in the lateral geniculate body of the rabbit 7 days after section of an optic nerve, in the form of end-plates, annular end-formations and boutons. However, he apparently did not study the normal geniculate body of this animal, nor was he concerned with the nature of the normal terminations of the optic fibres in the nucleus.

In a comprehensive monograph on the lateral geniculate body, Balado & Franke (1937) state that in Man the number of cells in the lateral geniculate body is about the same as the number of optic fibres. If this is so, the numerical relation of fibres to cells is very different to that which has been observed in other mammals. However, it is not possible to assess the accuracy of their statement, for Balado & Franke give no details of the methods they used to enumerate the cells in the lateral geniculate body. Also, for a fibre estimate they depended on a count of fibres in the optic nerve although, of course, many of these fibres are destined for the mid-brain and do not end in the lateral geniculate body.

One of the results of this study of the lateral geniculate body has been to provide the first *direct* evidence that crossed and uncrossed retinal fibres end in different cell laminae.<sup>1</sup> That is to say, crossed fibres end in laminae 1, 4 and 6, while uncrossed fibres end in laminae 2, 3 and 5.

#### SUMMARY

1. Seven days after section of one optic nerve in the monkey, the corresponding laminae in the lateral geniculate body are filled with thickened terminal fibres and enlarged and deeply staining boutons. These laminae therefore stand out in strong contrast with the normal laminae which receive the terminal fibres of the intact optic nerve.

<sup>1</sup> This observation has already been recorded by one of us (P. G. 1940).

2. It is established that each main optic fibre commonly terminates in a spray of 5-6 branches, and therefore in relation to 5-6 geniculate cells. The boutons of the degenerated optic fibres lie in contact with the cell body, and no geniculate cell is related to more than one bouton.

3. By the study of the degenerating terminal fibres and boutons, direct evidence has been provided in confirmation of the conclusion, previously based on transneuronal atrophy, that crossed optic fibres end in laminae 1, 4 and 6 of the lateral geniculate body, while uncrossed fibres end in laminae 2, 3 and 5.

Grateful acknowledgement is made by one of us (P. G.) for the assistance of a grant from the Nuffield Committee for the Advancement of Medicine.

## REFERENCES

- BALADO, M. & FRANKE, E. (1937). *Das Corpus Geniculatum Externum*. Berlin.  
 BARNARD, R. I. (1940). *J. comp. Neurol.* **73**, 235.  
 BARR, M. L. (1940). *J. Anat., Lond.*, **74**, 1.  
 BARRIS, R. W. (1935). *Arch. Ophthalm., N.Y.*, **14**, 61.  
 BIELSCHOWSKY, M. (1935). *Handb. Neurol.* **1**, 35.  
 BROUWER, B. (1923). *Schweiz. Arch. Neurol. Psychiat.* **13**, 118.  
 BROUWER, B. & ZEEMAN, W. P. C. (1925). *J. Neurol. Psychopath.* **6**, 1.  
 CAJAL, S. R. (1911). *Histologie du Système Nerveux*. Paris.  
 — (1935). *Handb. Neurol.* **1**, 887.  
 CATTANEO, D. (1923). *Riv. Patol. nerv. ment.* **28**, 61.  
 CLARK, W. E. LE GROS (1932). *Brit. J. Ophthalm.* **56**, 264.  
 — (1941). *J. Anat., Lond.*, **75**, 225.  
 CLARK, W. E. LE GROS & PENMAN, G. G. (1934). *Proc. roy. Soc. B*, **114**, 291.  
 FOERSTER, O., GAGEL, O. & SHEEHAN, D. (1933). *Z. Anat. EntwGesch.* **101**, 553.  
 GIBSON, W. C. (1937). *Arch. Neurol. Psychiat., Lond.*, **38**, 1145.  
 GLEES, P. (1940). *Nature, Lond.*, **146**, 747.  
 HECHST, B. (1933). *Arch. Psychiat. Nervenkr.* **100**, 19.  
 HENSCHEN, S. E. (1897, 1898). *Neurol. Zbl.* **16** and **17**.  
 — (1924). *Trav. Lab. Recherches Biol. Univ. Madrid*, **22**, 217.  
 HOFF, E. C. (1932). *Proc. roy. Soc. B*, **111**, 175.  
 KÖLLIKER, A. (1896). *Lehrbuch der Gewebelehre*, **2**, 585.  
 METTLER, F. A. (1935). *J. comp. Neurol.* **61**, 221.  
 MINKOWSKI, M. (1920). *Schweiz. Arch. Neurol. Psychiat.* **6**, 201.  
 PHALEN, G. S. & DAVENPORT, H. A. (1937). *J. comp. Neurol.* **68**, 67.  
 POLIAK, S. (1932). *Univ. Calif. Publ. Anat.* **2**, 14.  
 — (1933). *J. comp. Neurol.* **57**, 541.  
 RÖNNE, H. (1913). *v. Graefes Arch. Ophthalm.* **85**, 489.  
 — (1914). *Z. ges. Neurol. Psychiat.* **22**, 469.  
 SCHIMMERT, J. (1938). *Z. Anat. EntwGesch.* **108**, 761.  
 TELLO, J. F. (1904). *Trab. Lab. Invest. biol. Univ. Madr.* **3**, 39.  
 WALKER, A. E. (1938). *J. belge Neurol. Psychiat.* **2**, 89.  
 WHITNALL, S. E. & NORMAN, R. M. (1940). *Brit. J. Ophthalm.* May, 229.  
 WINKLER, C. (1912). *K. Akad. Wet. Amst.* **15**.  
 — (1913). *Opera Omnia*, **5**.

## EXPLANATION OF PLATES 1 AND 2

## PLATE 1

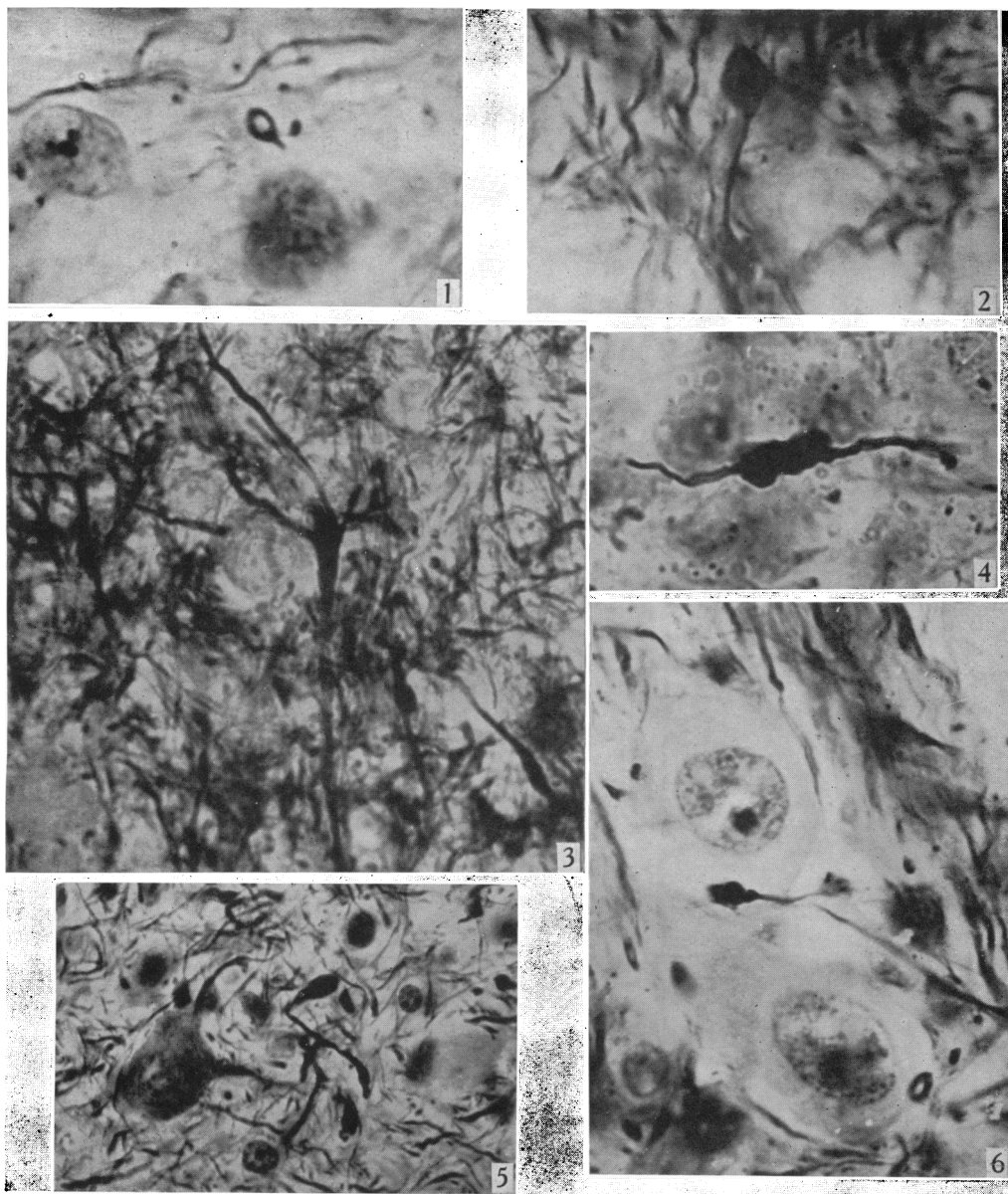
- Fig. 1. A terminal bouton of normal appearance in the lateral geniculate body.  $\times 1500$ .
- Fig. 2. A degenerating bouton from the lateral geniculate body of Experiment O.M. 502. The bouton is slightly enlarged, and the interior of the ring is filled with a fibrillar substance.  $\times 1850$ .
- Fig. 3. The axone terminal of an optic fibre from Experiment O.M. 502. Note the thickening of the fibre at the site of its division. From here, fine terminal branches can be seen proceeding.  $\times 630$ .
- Fig. 4. A degenerating axone in a fasciculus of the optic tract in Experiment O.M. 503.  $\times 900$ .
- Fig. 5. Degenerating terminal boutons in the geniculate body of Experiment O.M. 503. On the left, a bouton is seen lying in contact with the cell body of a geniculate cell. On the right two terminal branches of an optic fibre are seen ending in degenerating boutons.  $\times 400$ .
- Fig. 6. Two cells in the geniculate body of Experiment O.M. 503. In relation to the cell below is an apparently normal bouton, while a solid and irregularly shaped degenerating bouton lies in contact with the cell above.  $\times 1350$ .

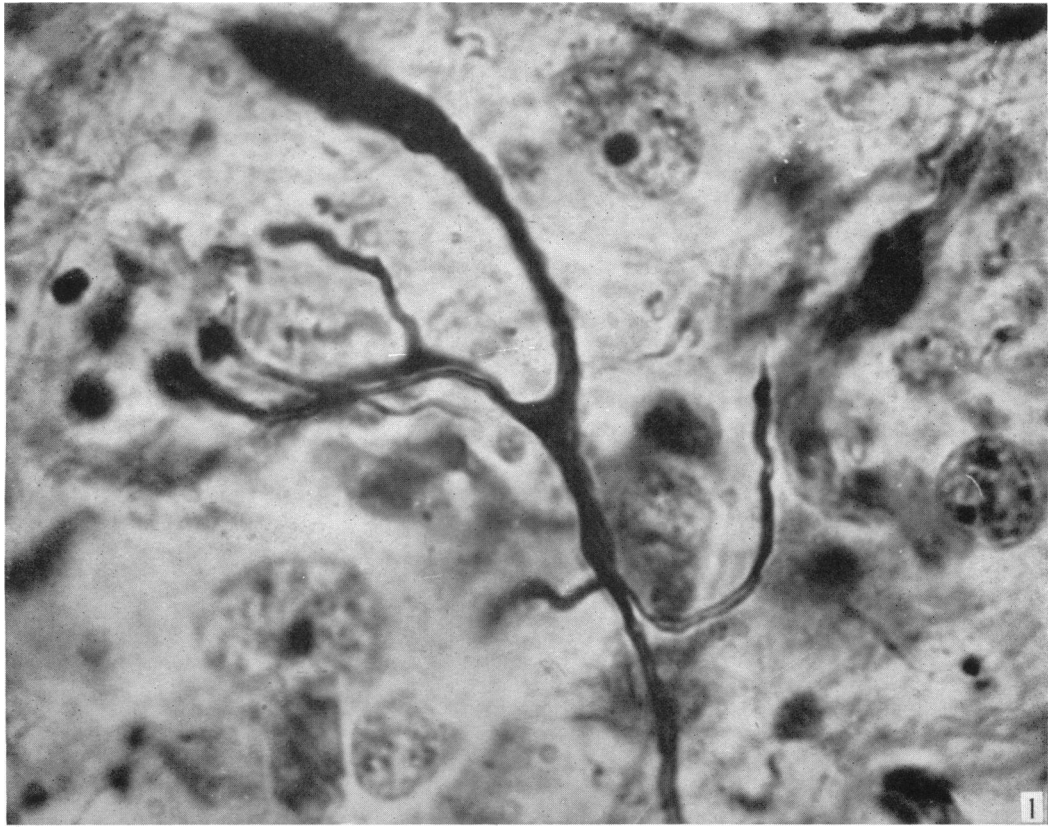
## PLATE 2

- Fig. 1. The degenerating terminal of an optic fibre from Experiment O.M. 503. Note the thickening of the fibre at the point of its division. The fibre divides into six terminal branches, and enlarged terminal boutons are seen on three of these.  $\times 1800$ .
- Fig. 2. Degenerating terminal optic fibres in the lateral geniculate body of Experiment O.M. 503. Note the irregular swelling of the fibres.  $\times 1400$ .

## ADDENDUM

Since this communication was sent to the press we have seen a recent paper by J. L. O'Leary on the lateral geniculate nucleus of the cat (*J. comp. Neurol.* **73**, 1940, 405). In this animal it was found that 'within a cellular lamina the terminal arborizations overlap each other ("partially shifted overlapping") so that each principal cell makes synaptic contacts with the terminals of several different optic tract fibres'. If this is the case, it appears to constitute a significant difference from the condition in the geniculate body of the monkey. It is to be noted, however, that O'Leary's observations (like those of Cajal and Tello) were made on Golgi preparations of normal material, so that they are not directly comparable with our own observations which are based on technical methods designed to show directly the relation of optic terminals to geniculate cells. The application of the Golgi technique to the lateral geniculate body of the monkey is limited by the lack of adequate and appropriate material in our laboratory, and such preparations as we have hitherto made fail to show a satisfactory impregnation.





**GLEES AND CLARK—TERMINATION OF OPTIC FIBRES IN THE MONKEY**